INTERACTIONS BETWEEN RESIDENT AND MIGRATORY WAGTAILS *MOTACILLA* SPP. IN ETHIOPIA - AN ECOLOGICAL CONUNDRUM

Stephanie J. Tyler and S.J. Ormerod

The co-existence of congeneric animals is frequently facilitated by factors which reduce competition for resources such as food, space or nest sites (see for example Branch 1976, Finlay & Berninger 1984, Hildrew & Edington 1979, Meserve 1976 and Schoener 1974). Lack (1971) reviewed many instances of such niche segregation between breeding birds; wherever ranges of habitats coincided, ecological isolation could occur by interspecific differences in micro-habitat occupation and/or feeding preferences (see Lack 1971, Perrins & Birkhead 1983). In some cases, direct competition results in interspecific aggression, mutual exclusion from breeding territories (e.g. Garcia 1983) and in 'niche-shifts' (e.g. Davis 1973, Alerstam *et al.* 1974). In other cases, breeding success may be impaired by the presence of close competitors (Minot 1981, Hogstedt 1980).

Little detailed attention has been given to interactions between Palaearctic migrants and congeneric residents in Africa (e.g. Lack 1971, Moreau 1972, Morel 1973). In Ethiopia, for example, the winter influx of Grey Wagtails *Motacilla cinerea*, Yellow Wagtails *M. flava* and White Wagtails *M. alba* leads to possible contacts with the resident African Pied *M. aguimp* and Mountain Wagtails *M. clara*. This paper reviews the distribution and habitat preferences shown by each species in Africa, particularly in Ethiopia. Where available, information is given on breeding biology and feeding ecology. Particular attention is given to interactions between *M. cinerea* and *M. clara*; these species show similar habitat preferences and co-occur at a time when *M. clara* is breeding.

SPECIES DISTRIBUTIONS

General distributions within Africa of resident and migrant *Motacilla* spp. were drawn from the literature. More specific accounts for Ethiopia were based on fieldwork between October 1973 and January 1977 mostly in the central province of Shewa. This province includes habitats ranging from desert at 1000 m O.D., rift valley lakes with *Acacia* woodland and savanna, and montane forest and moorland at over 3000 m.

Motacilla aguimp African Pied Wagtail

African distribution

The commonest wagtail in Africa, *M. aguimp* has a similar range to *M. clara* (see below). It occurs throughout the continent south of the Sahara, though it is absent from the Somali Republic and from the extreme west of Cape Province (Mackworth-Praed & Grant 1957). Several authors have noted an association with dwellings and settlements (Belcher 1930, Vincent 1935, Priest 1935, Benson 1940, Mackworth-Praed & Grant 1957, Elgood & Sibley 1964). It occurs throughout an altitudinal range from sea level to 3000 m and generally, alongside pools, ponds, swamps and particularly along larger rivers.

Distribution in Ethiopia
In Ethiopia, *M. aguimp* occurs locally everywhere except in the south-east (Urban & Brown 1971) and extreme north (Smith 1955). Most observations were on large but fast-flowing rivers below 2000 m (see also Cheeseman 1935, Smith 1957, Olson 1976). Breeding abundances of one pair per 1.6 km (Smith 1957) and up to four pairs per kilometre (this study) have been recorded.

Breeding Biology
Most breeding records were between February and July prior to the rains, and most clutches were of two to three eggs (c.f. Belcher 1930 and Priest 1935 who noted clutches of four to five eggs in southern Africa). Nest sites included rock ledges, holes in walls and bridge sites.

Motacilla clara Mountain Wagtail
African Distribution
From Liberia eastwards to Ethiopia; southwards to Cape Province *M.c. torrentium* and *M.c. chapini* have extensive ranges in Africa but the longer-winged nominate race is confined to Ethiopia. Over most of its range, *M. clara* favours small, often forested, fast-flowing mountain streams between 1250 and 3000 m; some observations at lower altitudes may reflect seasonal movements (Belcher 1930, Benson 1940, Winterbottom 1964, Serle 1950, Elgood 1973, Britton 1980).

Distribution in Ethiopia
In Ethiopia, *M. clara* is a montane species and there is no evidence for any seasonal movement to lower altitudes. It occurs on small, wooded highland rivers and streams from 1500 to 3400 m both north and south of the Rift Valley. In Shewa, it is found on those stretches of river favoured by the Abyssinian Black Duck *Anas sparsa*. In southern Tigre it was common and Olson (1976) found it frequent on the wooded streams in the Tana Basin, the Tacazze River and western escarpment of Begemder and Simien Province. In northern Tigre it was only observed twice between January and May 1976 despite searches along apparently suitable watercourses. These two records were on a wooded stream near Samre, southwest of Makalle, and near Enticho close to the Eritrean border. K. Thorogood (pers. comm.) did not record *M. clara* in northern Tigre from March 1973 to September 1975, and it was not seen in Eritrea (Smith 1955, 1957, this study).

Breeding Biology
Breeding was recorded in January to April and from September to November (c.f. Moreau 1949: all year; Winterbottom 1964: August to December). Forty-five nest sites included cliff ledges, banks overhanging water, bankside roots, holes in walls and recesses in bridges; generally similar to those used by *M. cinerea* in Britain (Tyler 1972).

Six nests contained clutches of 2 eggs, although two parties of 3 fledged young were seen. Other studies elsewhere in Africa indicate a clutch size of 2-3 (occasionally 4)(Moreau 1949, Belcher 1930, Winterbottom 1936, 1964, Piper 1982). One nest which was regularly observed gave an incubation period of 13 days (c.f. Moreau 1949: 14

days) and a fledging period of 15-16 days. Juvenile dependency varied from 14-30 days.

Food and feeding behaviour
Food items taken by *M. clara* included larval and adult dipterans, other winged insects such as mayflies and dragonflies and larvae or nymphs of aquatic invertebrates.

Birds fed by flycatching over water, picking and run-picking from the river edge or from rocks. Birds were also observed walking in shallow water and catching tadpoles, and one pair when feeding juveniles caught numerous large dragonfly nymphs; each was clubbed against a rock prior to being fed to the young.

M. cinerea Grey Wagtail
African Distribution
In Africa *M. cinerea* breeds only in Morocco where it is abundant up to 9000 feet (2700 m) (Chalworth-Muster 1939).

The main wintering area is in the northeast and east, some birds crossing the equator. *M. cinerea* has been recorded regularly from Malawi (Benson *et al.* 1971, Benson & Benson 1977), occasionally from southern Zambia and Natal and recently from Zimbabwe (Williams 1984). Few occur in West Africa but some do penetrate to 2 N in northeastern Zaire and appear along streams and tracks in forests (Moreau 1972). In the Sudan, Ethiopia, Uganda, Kenya and northeastern Tanzania, birds are widespread in the winter on fast-flowing, wooded mountain streams from 1500 to 3000 m. Further north they occur at low altitudes in oases of the Sahara and in the Arabian Gulf.

Distribution in Ethiopia
M. cinerea was found to be common in Ethiopia on those highland streams and rivers favoured by *M. clara*. It occurred also in a variety of other habitats such as around farms, sewage pits, forest tracks, moist grassland and along larger rivers. It was most frequent between 1500 and 3000 m, but was observed in the Simien Mountains at almost 4000 m and in Tigre province at the foot of the escarpment on a lowland river below 1000 m. Friedmann (1937) recorded *M. cinerea* in Abyssinia only above above 4000 feet (1220 m) and quoted Mearns as finding it as high as 10 000 feet (3050 m). In Eritrea Smith (1957) found *M. cinerea* to be a regular winter visitor to dams, escarpment streams and, in Dancalia (below 500 m), he often observed it far from water in *Combretum* woodland and sometimes dry *Acacia*.

M. cinerea was one of the earliest Palaearctic migrants to arrive in Ethiopia. Daily observations in a wadi in northeast Eritrea from June 1976 to January 1977 showed the first *M. cinerea* on 12 August (Tyler 1978). One to three birds were noted on most days up to 10 October, with a maximum of eight birds on an 800 m stretch of a small stream flowing down the wadi. Two birds on 27 October were the last recorded. In eastern Ethiopia Dr J.S. Ash (pers. comm.) recorded an early migrant on 1 September but in the Shewan highlands birds were not seen until mid-September with the first record in Addis Ababa on

18 September (this study). In the spring, they left the highlands during March although some remained until early April. Smith's (1957) latest records were in Eritrea on 13 April.

Food and feeding behaviour
M. cinerea fed in the same manner as *M. clara* and appeared to be taking the same prey items - benthic invertebrates and adult winged insects. In Eritrea birds were observed feeding in a very shallow stream, pecking repeatedly at blackfly *Simulium* larvae which were abundant.

Motacilla alba White Wagtail
African Distribution
The Palaearctic White Wagtail occurs across northern tropical Africa during the northern winter with a few birds reaching Zambia and Malawi (Benson *et al.* 1971). Numbers appear to be relatively few in West Africa (Moreau 1972).

Distribution in Ethiopia
Ethiopia is one of the main wintering areas; *M. alba* is common from the coast to over 2500 m between October and March. The earliest dates of arrival are 14 October (Smith 1957) and 20 October (Tyler 1978) in Eritrea; the latest record is 8 April (Ash 1980).

M. alba utilizes a greater range of habitats than other species of wagtail. It may be found around buildings in towns and villages, by lakes, streams and rivers, muddy pools, irrigation ditches, vegetable patches and farmyards, desert wells and damp grassland, either singly or in small groups. A flock of up to 19 birds wintered in a wadi in northeast Eritrea in 1976/77 (Tyler 1978).

Motacilla flava Yellow Wagtail
African Distribution
This species winters across Africa and as far south as Zambia with different races favouring different parts of the continent (see Wood 1976). Sudan, Ethiopia and northern Kenya are the main wintering area for several races.

Distribution in Ethiopia
A number of races occur throughout Ethiopia between late August and June; some, such as *M.f. lutea*, are passage migrants. Urban & Brown (1971) accepted six races - *flavissima, flava, beema, thunbergi, lutea* and *feldegg*. Previous *flavissima* records may, however, have been confused with *lutea* (see Moreau 1972 and Pearson & Backhurst 1973). Smith (1957) determined five races in Eritrea - *flava* (including *beema* and *dombrowski, lutea, thunbergi, feldegg* and *superciliaris*. He found the last to be fairly common on passage along the coastal plain between February and April; Pain, Tyler & Vittery (1975) recorded one bird in Addis Ababa. Mixed flocks of *flava, thunbergi* and *feldegg* occurred with *feldegg* often predominating on the coastal plain and on the plateau in Eritrea (Smith 1957). *M.f. feldegg* was also common in Tigre, sometimes occurring singly

alongside open streams (this study) but further south *M.f. flava* was most abundant. Wallace (1955) noted that *feldegg* preferred wetter habitats than other races.

Yellow Wagtails occurred in large numbers on the highland plateau feeding in flocks on open grassland, usually with herds of cattle or goats or flocks of sheep; they also accompanied domestic animals or game in savanna and around lake shores in the Rift Valley. At the edge of Koko Reservoir in the northern Rift Valley, they fed alongside Red-throated Pipits *Anthus cervinus* and Richard's Pipits *A. novaeseelandiae*. Associations of *M. flava*, *A. cervinus* and Ortolan Buntings *Emberiza hortulana* were recorded by slow-flowing highland rivers and on other muddy ground, where these species came into contact with *M. alba*. Wood (1976) noted that in Nigeria, *A. cervinus* was the only real competitor of *M. flava*.

SPECIES INTERACTIONS WITHIN ETHIOPIA

The presence in Ethiopia of five *Motacilla* species during the northern winter provides for possible interactions. At least for *M. aguimp*, *M. alba* and *M. flava*, there is sufficient habitat segregation and plasticity to prevent inter-specific competition (Table 1). Casual observations, however, indicated that *M. clara* and *M cinerea* were less clearly segregated by habitat or feeding behaviour and a more specific study on these species was initiated.

TABLE 1

Habitat preferences shown by resident and migrant Motacilla *spp. in Ethiopia during the northern winter*

Species	Preferred habitat	altitudinal distribution
M. aquimp	Lakes, pools, larger rivers, occasionally pastures	50-2000 m
M. clara	Small, wooded highland rivers	1500-3500 m
M. cinerea	Small, wooded highland rivers, occasionally other wet habitats	1500-3000 m
M. alba	Highly plastic; towns, villages and all wet habitats	0-2500 m
M. flava	Drier grassland than *M. alba* or *M. aguimp*; often with domestic stock	0-3000 m

Detailed observations were made between March 1974 and March 1975 of territoriality and interactions between *M. clara* and *M. cinerea*. Most data were from three highland rivers (1750-2500 m) supplemented by data from streams at Sebeta and Meta west of Addis Ababa (Table 2).

TABLE 2
Territories held by M. clara *and* M. cinerea *on some Ethiopian rivers*

River	Length surveyed (m)	*M. clara* Pairs	*M. clara* Average length of territory	*M. cinerea* Individuals	*M. cinerea* Average length of territory
Akaki (Addis Ababa)	1300	2	650	7	186
Ambo (120 km west of Addis)	1600	6-7	228-267	6	267
Bole valley	2500	9-12	208-277	12	208
Meta (west of Addis)	600	1	600	5	120
Sebeta (west of Addis)	700	1	700	4	125
Romanat Falls (Tigre)	600	-	-	3	200

There was some evidence that the two species were partly mutually exclusive, with *M. cinerea* occurring in greatest numbers where *M. clara* was relatively scarce (Fig. 1). Nevertheless, few interspecific territorial encounters were witnessed and individuals from each species frequently fed in close proximity, even on the same rock. In the Bole Valley during March 1975, mixed feeding groups consisting of four to five *M. clara* (fledged young plus adults) and one *M. cinerea* were commonly seen. Other accounts confirm the tolerance shown between these species (Winterbottom 1964, Moreau 1972, Williams 1984), although they are strongly intraspecifically aggressive.

DISCUSSION

At least for three of the five *Motacilla* spp. present in Ethiopia during the northern winter, fairly clear habitat preferences prevent any direct competition (Table 1). By contrast, the apparently close association between *M. clara* and *M. cinerea*, without obvious interspecific aggression, represents a subject for further research. Most breeding pairs of *M. clara* tolerated *M. cinerea* within their territories. Moreover, *M. clara* is structurally very similar to *M. cinerea*

and its slightly larger bill is probably not sufficiently different for the two to coexist and not compete for the same food (B. Wood, pers. comm.).

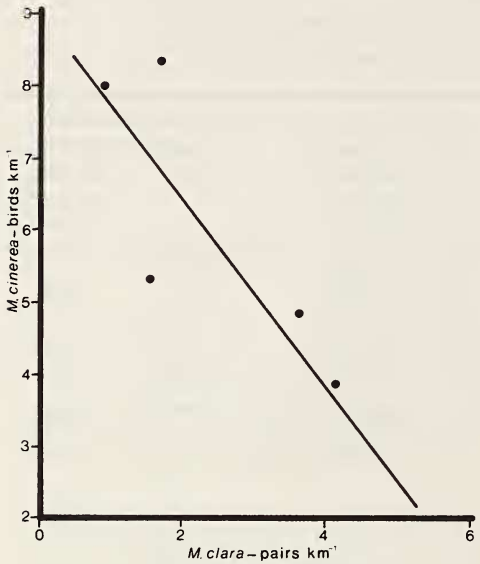

Fig. 1. The abundances of breeding *M. clara* and migrant *M. cinerea* along five rivers in Ethiopia. The line was fitted by eye.

Moreau (1966) suggested that Palaearctic migrants might be accomodated within the Afrotropical region during the northern winter due to a seasonal superabundance of food. Other breeding passerines have been shown to coexist where food is abundant despite showing little ecological segregation (Blancher & Robertson 1984). Alternatively, the available food may be non-depressible (Charnov *et al.* 1976). Whilst few quantitative data are available on the benthic invertebrates of highland streams in Ethiopia, those in regions with similar climate and physiography have been described (Williams & Hynes 1971, Hynes 1975). The greatest invertebrate abundances accompany the end of the rainy season and groups such as the Simuliidae predominate. Consequently, an abundant and readily available food supply is likely to occur when *M. cinerea* arrives in Ethiopia and when *M. clara* is breeding. Nevertheless, some degree of mutual exclusion (Fig. 1) seemed apparent and the breeding performance of *M. clara* should be compared between territories with and without co-occurring *M. cinerea* (Hogstedt 1980, Minot 1981). Additional quantitative data are also required on the food taken by each species.

ACKNOWLEDGEMENTS

One of us (SJT) was in receipt of a grant of £50 from the British Ornithologists' Union and we are grateful for this contribution

towards the fieldwork. The encouragement and help from Dr John S. Ash and Mr Lindsay Tyler is also acknowledged.

REFERENCES

ALERSTAM, T., NILSSON, S.G. & ULFSTRAND, S. 1974. Niche differentiation during winter in woodland in birds in southern Sweden and the island of Gotland. *Oikos* 24: 321-330.

ASH, J. 1980. Migrational status of Palaearctic birds in Ethiopia. *Proceedings of the Fourth Pan-African Ornithological Congress held at Mahé, Seychelles 6-13 November 1976*. Southern African Ornithological Society.

BELCHER, C.F. 1930. *The Birds of Nyasaland*. London: The Technical Press.

BENSON, C.W. 1940. Nyasaland Birds. *Ibis* 14: 585-587.

———— & BENSON, F.M. 1977. *Birds of Malawi*. Limbe: Montford Press.

BLANCHER, P.J. & ROBERTSON, R.J. 1984. Resource use by sympatric kingbirds. *The Condor* 86: 305-313.

BRANCH, C.M. 1976. Interspecific competition experienced by South African *Patella* species. *Journal of Animal Ecology* 45: 507-531.

CHALWORTH-MUSTER, J.L. 1939. Birds of the High Atlas of Morocco. *Ibis* 14: 273.

CHARNOV, E.L., ORIANS, G.H. & HYATT, K. 1976. Ecological implications of resource depression. *American Naturalist* 110: 247-259.

CHEESEMAN, R.E. & SCLATER, W.L. 1935. On a collection of birds from north-western Abyssinia. *Ibis* 13: 163-197.

DAVIS, J. 1973. Habitat preferences and competition of wintering juncos and golden-crowned sparrows. *Ecology* 54: 174-180.

ELGOOD, J.H. 1973. African migrants in Nigeria. *Ibis* 115: 375-411.

———— & SIBLEY, F.C. 1964. The tropical forest edge avifauna of Ibadan, Nigeria. *Ibis* 106: 221-248.

FINLAY, B.J. & BERNINGER, U.G. 1984. Co-existence of congeneric ciliates (Karyorelictida: Loxodes) in relation to food resources in two freshwater lakes. *Journal of Animal Ecology* 53: 929-945.

FRIEDMANN, H. 1937. Birds collected by the Childs Frick Expedition to Ethiopia and Kenya Colony. Part 2. Passeres. *Bulletin of the United States National Museum* 153: 1-506.

GARCIA, E.F.J. 1983. An experimental test of competition for space between Blackcaps *Sylvia atrocapilla* and Garden Warblers *Sylvia borin* in the breeding season. *Journal of Animal Ecology* 52: 795-807.

HILDREW, A.G. & EDINGTON, J.M. 1979. Factors facilitating the co-existence of hydropsychid caddis larvae in the same river system. *ibidem* 48: 557-576.

HOGSTEDT, G. 1980. Prediction and test of the effects of interspecific competition. *Nature, London* 283: 64-66.

HYNES, J.D. 1975. Downstream drift of invertebrates in a river in southern Ghana. *Freshwater Biology* 5: 515-532.

LACK, D. 1971. *Ecological isolation in Birds*. Oxford: Blackwell.

MESERVE, P.L. 1976. Habitat and resource utilization by rodents of a Californian coastal sage scrub community. *Journal of Animal Ecology* 45: 647-667.

MINOT, E.O. 1981. Effects of interspecific competition for food on breeding Blue and Great Tits. *Journal of Animal Ecology* 50: 375-385.

MOREAU, R.E. 1949. The African Mountain Wagtail at nest. Ornithologie als biologische Wissenschaft (Festschrift zum 60. Geburtstag von Enwin Stresemann) pp. 183-191. Ed. E. Mayr & E. Schüz.

MOREL, G. 1973. The Sahel Zone as an environment for Palaearctic migrants. *Ibis* 115: 413-417.

OLSON, C. 1976. Summary of field observations of birds from Begemder and Simien province. *Walia* No. 7: 16-27.

PAIN, H., TYLER, S.J. & VITTERY, A. 1976. *A Checklist of the Birds of Addis Ababa*. Ethiopian Wildlife & Natural History Society.

PEARSON, D.J. & BACKHURST, G.C. 1973. The head plumage of eastern yellow-headed Yellow Wagtails wintering at Nairobi, Kenya. *Ibis* 115: 589-591.

PERRINS, C.M. & BIRKHEAD, T.R. 1983. *Avian Ecology*. Glasgow & London: Blackie.

PIPER, S.E. 1982. Five years of wagtailing. *Safring News* 11(1): 5-8

PRIEST, C.D. 1935. *The Birds of Southern Rhodesia*. London & Beccles: William Clowes & Sons.

SCHOENER, T.W. 1974. Resource partitioning in ecological communities *Science* 185: 27-39.

SERLE, W. 1957. A contribution to the ornithology of the eastern region of Nigeria. *Ibis* 99: 371-418, 628-685.

———— 1950. A contribution to the ornithology of the British Cameroons. *Ibis* 92: 369.

SMITH, K.D. 1955. Recent records from Eritrea. *Ibis* 97: 65-80.

———— 1957. An annotated check list of the birds of Eritrea. *Ibis* 99: 307-337.

TYLER, S.J. 1972. Breeding biology of the Grey Wagtail. *Bird Study* 19: 69-80.

———— 1978. Some observations of birds in Fah, northeast Eritrea. *Bulletin of the British Ornithologists' Club* 98: 80-87.

URBAN, E.K. & BROWN, L.H. 1971. *A Checklist of the Birds of Ethiopia*. Addis Ababa: Haile Selassie I University Press.

VINCENT, J. 1935. The Birds of Portugese East Africa. *Ibis* 13.

WALLACE, D.I.M. 1955. The mixing of the races of the Yellow Wagtail in Kenya. *British Birds* 48: 337-340.

WILLIAMS, J. 1984. Grey Wagtail at Nyanga. *The Honeyguide* 30(2): 77.

WILLIAMS, T.R. & HYNES, H.B.N. 1971. A survey of the fauna of streams on Mount Elgon, East Africa, with special reference to the Simuliidae (Diptera). *Freshwater Biology* 1: 227-248.

WINTERBOTTOM, J.M. 1936. Distributional and other notes on some Northern Rhodesian birds. *Ibis* 13: 776.

———— 1964. Notes on the wagtails of southern Africa. *Ostrich* 35: 129-141.

WOOD, B. 1976. The Biology of Yellow Wagtails *Motacilla flava* L. overwintering in Nigeria. Ph.D. Thesis. University of Aberdeen.

Stephanie J. Tyler, Royal Society for the Protection of Birds, Wales Office, Frolic Street, Newtown, Powys SY16 1AP, Wales, and *S.J. Ormerod, Department of Applied Biology, University of Wales Institute of Science and Technology, King Edward VII Avenue, Cathays Park, Cardiff, Wales.*

(Received 23 August 1985)

REQUEST FOR INFORMATION

Between 1970 and 1975 I ringed almost 2000 birds in the Kakamega Forest and adjacent parts of the South Nandi Forest. The vast majority were resident forest species and many were controlled frequently. Since leaving East Africa eleven years ago I have received almost no information on the retrapping of these birds. However, I know that a number of ornithologists have been active with mist nets in the area since that time and could not avoid capturing some of my birds. I would have expected anyone capturing a ringed bird to be curious enough to report it to the Ringing Organizer to discover the details of its original capture. This seems not to have happened. That some of the birds are almost certainly alive in the area is evidenced by the fact that in January 1985 Dr Simon Cox captured one of my birds first ringed in 1974, and one ringed by D.A. Zimmerman in 1965, in just a few hours of netting.

Anyone who has information is encouraged to contact me at the address given. Any retrap details will be very gratefully received and acknowledged, and I will supply the original ringing details.

Clive F. Mann, P.O. Box 2359, Bandar Seri Begawan, State of Brunei.